Fundam. appl. Nematol., 1995, **18** (5), 407-417

Forum article

AN ASSESSMENT OF THE RELEVANCE OF THERMAL TIME RELATIONSHIPS TO NEMATOLOGY

David L. TRUDGILL

Scottish Crop Research Institute, Invergowrie, Dundee DD2 5DA, Scotland, UK.

Accepted for publication 30 September 1994.

Summary – The requirements and problems of conducting thermal time studies are discussed and the utility of fitting a linear relationship between temperature and rates of nematode embryogenesis and development is reviewed. Published data on durations of development at different temperatures, for a range of nematodes including animal parasitic species, are converted to rates of development and base temperatures (T_b) and thermal constants (S, expressed as °C day requirements above T_b) are estimated. New data on the minimum requirements for embryogenesis in *Meloidogyne javanica* are compared with the minimum requirements for a complete life cycle. The ecological significance of differences in the value of T_b and S are considered and it is proposed that, for comparable species (*M. hapla* and *M. javanica*), as the value of T_b increases so the value of S decreases.

Résumé – ***Évaluation de la pertinence des relations entre durée et température en nématologie*** – Les données nécessaires et les problèmes concernant la conduite d'études sur la température sont discutés et l'utilité d'un ajustement à une relation linéaire entre température d'une part et taux d'embryogenèse et de développement d'autre part est passée en revue. Les données publiées sur la durée du développement à différentes températures d'un éventail de nématodes incluant des espèces zooparasites sont converties en taux de développement et il est produit une estimation de la température de base (T_b) ainsi que des constantes thermiques (S, exprimé en degrés C/jours nécessaires au-dessus de T_b). De nouvelles données concernant les besoins minimum pour l'embryogenèse de *Meloidogyne javanica* sont comparées avec les besoins minimum pour un cycle complet. La signification écologique des différences entre les valeurs de T_b et de S sont prises en compte et il est proposé de considérer que, pour des espèces comparables (ici *M. hapla* et *M. javanica*), lorsque la valeur de T_b augmente celle de S. diminue.

Key-words : *Heterodera, Globodera, Meloidogyne, Longidorus, Xiphinema, Ostertagia, Haemonchus, Caenorhabditis,* " r " and " K " strategists, embryogenesis, generation time, threshold or base temperature, thermal constant, ecology.

Tyler (1933 *a*) was the first to apply a thermal-time analysis to the development of plant parasitic nematodes. She regressed the rate of development (expressed as the reciprocal of the minimum time for one generation) of an unknown *Meloidogyne* spp. *(Heterodera marioni)* against temperature and showed that the relationship was close to linear over a wide range of temperatures. A threshold or base temperature (T_b) for development can be estimated by back projection of the linear regression line to where it intercepts the temperature axis. This gave a T_b of between 10 and 11.5 °C, a value of considerable ecological significance as will be discussed later. As the relation is linear, the minimum thermal time or heat sum requirement for one generation (S, measured as the reciprocal of the slope and expressed in °C days) is a constant (S = *c.* 300 °C days with T_b = 10 °C). This value is also of considerable ecological significance as it reflects the amount of development to be done divided by the rate. The optimum temperature (T_o) for development of this *Meloidogyne* spp. was close to 28 °C, above which the rate of development rapidly decreased towards zero at a maximum temperature (T_m). Between T_b and T_o the duration of development (D) is :

$$D = \frac{S}{T_e - T_b} \qquad \text{(equation 1)}$$

where T_e is the mean environment temperature.

As Tyler (1993 *a*) stated " it is well known that invertebrate animals are dependent on the temperature of their environment for their vital activities ". Consequently, thermal time studies have been conducted on many poikilothermic organisms, including plants. Thermal time information can be extremely useful for a number of reasons, including the ability to calculate temperature effects on durations of processes of economic significance. For many crop plants a linear relationship between temperature and rate of development (for the temperature range T_b to T_o) has been established for several processes, e.g. rates of seed germination in many crops and leaf initiation in celery (Garcia-Huidobro *et al.* 1982; Ramin & Atherton, 1991), and thermal time information is used to calculate sowing dates which will

Table 1. *Estimated base temperatures* (T_b) *and thermal constants* (S) *for different nematodes.*

Species	Developmental process	T_b (°C)	S (°C days)	% variation accounted for (r^2)	Reference
Plant parasites					
*G. pallida**	J2 to ♂	3.93	272	99.7	Mugniéry (1977)
*G. rostochiensis**	J2 to ♂	6.23	204	99.8	Mugniéry (1977)
*G. pallida**+	Embryogenesis	4.5-6.8	123-120	> 99.4	Langeslag *et al.* (1982)
*G. rostochiensis**+	Embryogenesis	5.9-6.3	126-141	> 99.7	Langeslag *et al.* (1982)
H. cruciferae	J2 to J2	5.5	632	99.1	Koshy & Evans (1986)
H. cajani	J2 to J2	11.0	324	92.2	Singh & Sharma (1994)
*H. schachtii***+	J2 to J2	4.6	502	98.5	Griffin (1988)
L. elongatus	Embryogenesis	8.5	154	98.9	Boag (1985)
M. arenaria	Embryogenesis	10.11	176	99.0	Ferris *et al.* (1978)
M. hapla	J2 to J2	8.25	554	99.97	Lahtinen *et al.* (1988)
M. javanica	J2 to J2	13.1	343	99.3	Trudgill (1994)
M. javanica	Embryogenesis	13.0	138	98.1	Trudgill (1994)
Meloidogyne spp.	J2 to J2	10.0	300	–	Tyler (1933)
X. diversicaudatum	Embryogenesis	7.6	268	94.7	Flegg (1969)
Animal parasites					
H. contortus (Scotland)	Embryogenesis	6.6	14.9	99.9	Silverman & Campbell (1958)
H. contortus (Bristol)	Embryogenesis	9.1	13.9	99.7	Crofton *et al.* (1965)
H. contortus (Cornell)	Embryogenesis	13.0	11.8	98.5	Crofton *et al.* (1965)
O. circumcincta (Bristol)	Embryogenesis	4.1	16.5	97.8	Crofton & Whitlock (1964)
O. circumcincta (Cornell)	Embryogenesis	7.9	14.6	96.6	Crofton & Whitlock (1964)
Free-living					
A. avenae	Embryogenesis	8.3	31.0		Taylor (1962)
C. elegans	J1 to J1	5.3	43.1	99.7	Grewel (1991)
G. ulmi	J1 to J1	0.9	114	99.7	Leach *et al.* (1986)

\+ More than one population.

* Values fitted by the authors. All other values determined here by fitting linear regressions using " least squares " method.

** Griffin (1988) calculated a mean T_b value for *H. schachtii* of 6.3 °C rather than the 4.6 °C estimated here. The lower value here may be due to inaccuracies associated with deriving his data points from a histogram.

give a succession of harvest dates with certain vegetables. However, in insects the general view is that up to T_o, the relationship between rates of development and temperature is slightly sigmoidal (Wigglesworth, 1965), preventing the estimation of T_b and of S. However, a linear relationship proved satisfactory for expressing the winter development of the aphid *Sitobion avenae* (Williams & Wratten, 1987) but its summer development rate was curvi-linear close to T_o (Dean, 1974). However, re-plotting Dean's data for *Metopolophium dirhodum* and *Rhopalosiphum padi* gave good linear regressions between 10 °C (the lowest temperature tested) and T_o. Tyler (1993 *b*) also noted that the relationship for the nematode *H. marioni* might be slightly sigmoidal and Jones (1977) re-analysed data on the life cycle duration of *Mononchus aquaticus* and the relationship is clearly curvi-linear (sigmoidal), especially at the temperature extremes. Greet (1978) demonstrated a similar curvilinear relationship for *Panagrolaimus rigidus*. As will be discussed later, whether the relationship appears to be a straight line or to be sigmoidal may depend upon several factors, including the precision of the data, the heterogeneity of the population under test, temperature effects on adult size and whether the organism is capable of thermal adaptation.

Following Tyler's (1933) study, and in spite of both the potential theoretical and practical values of estimates of T_b and of S, thermal time relationships were largely ignored by plant nematologists for more than 40 years until Mugniéry (1977) demonstrated a linear relationship with temperature for the rate of development of males of potato cyst nematodes (or PCN : *Globodera rostochiensis* and *G. pallida*). The average values obtained for T_b and S, and the percentage variation ac-

counted for by a linear regression, for this and the other studies considered here are given in Table 1. Subsequently, Langeslag *et al.* (1982) showed a similar linear relationship for embryogenesis for both species of PCN. Singh and Sharma (1994) used a linear relation to estimate for *Heterodera cajani* a T_b of *c.* 11 °C and an S of *c.* 324 °C days for one generation on pigeon pea, although with only four temperatures and slightly variable data these values need confirmation. Koshy and Evans (1986) made observations at weekly intervals to determine the duration of development to first egg hatch of *Heterodera cruciferae*. Their data is relatively linear and gives a T_b of *c.* 5.5 °C and an S of *c.* 632 °C days (Table 1). Ferris *et al.* (1978) also demonstrated a linear relationship between temperature and the rate of embryogenesis of *Meloidogyne arenaria* and used it as part of a population dynamics/yield loss model. A linear relationship was similarly shown to apply to the minimum generation time of *M. hapla* and of *M. javanica* by Lahtinen *et al.* (1988) and Madulu and Trudgill (1994) respectively and to the bacterial feeding nematode *Goodeyus ulmi* (Leach *et al.*, 1986).

This paper covers several areas. It reviews the evidence for a linear or a sigmoidal relation between rates of nematode development and temperature. Although a linear thermal time relationship appears to apply to many nematode species, several authors with temperature/duration of development data have not assessed the linearity of the relationship between temperature and rate of development. Their data has been abstracted here and rates of development have been calculated and regressed against temperature to further investigate the utility of the thermal time relationship. Some of the methodological requirements for conducting thermal time studies are also considered. New data on *M. javanica* is presented which seeks to determine whether embryogenesis and the whole life cycle have the similar or different T_b values. Finally, the available data is considered in relation to the ecological significance of T_b and of S.

Methodological considerations

Thermal time studies require accurate measurement and recording of temperature. In many studies, especially those in incubators with lights, the pot/Petri dish temperature can be well above the air temperature because of radiant effects. Also needed are clear start and end points for the process whose duration, and hence rate is being determined. The end point in seed germination and many entomological studies is often given by 50 % germination or hatch, etc. but in nematode studies hatch of the first juvenile is often used, although Langeslag *et al.* (1982) determined the requirements for embryogenesis of 50 % of PCN eggs. The end point chosen will often affect the estimated value of S and may affect T_b.

A problem with some studies, and hence data interpretation, is a tendency for the magnitude of the errors to increase at the extremes. As the environnement temperature (T_e) increases to the optimum (T_o), so the duration of development decreases. Hence, unless the frequency of observations/sampling is correspondingly increased, the proportional error component associated with the delay in detecting the end point tends to increase. Equally, as the temperature approaches the base (T_b) any error in temperature measurement has a proportionally increasing effect. For example, at a T_e of 1.0 °C above T_b a 0.1 °C error in temperature measurement represents a 10 % error overall, but only a 1 % error at a T_e of 10.0 °C above T_b. For this reason, and the extended duration of studies at temperatures close to T_b, the value of T_b is usually determined by back extrapolation to the zero development rate. Consequently the linearity of the relationship close to T_b is often unproven. Similarly, it is often difficult to accurately estimate the thermal optimum (T_o), and rates of development may plateau, before decreasing rapidly as the environment temperature (T_e) approaches the thermal maximum (T_m).

A further consideration is that development will be slowed, and hence S increased, if environmental factors other than T_e are variable and, hence sometimes suboptimal. Consequently, fitting a line to a scatter of points is likely to over-estimate T_b. Hence, for the accurate estimation of T_b and S it is essential to determine accurately the mean temperatures and the start and end points, to have data spanning a wide range of T_e values, and to provide an optimal or constant environment. Also, development must be continuous, and not involve a diapause or be influenced by environmental cues such as hatching factors, chilling requirements, photoperiodism, etc.

Analysis of published data on durations of development

Flegg (1969) determined the duration of embryogenesis (to hatching) at five temperatures of eggs excised from *Xiphinema diversicaudatum*. Re-plotting these durations as rates (Fig. 1) produced points to which a slightly sigmoidal curve or a straight line can be reasonably fitted. A straight line fitted by the " least squares " method (Table 1) gave values of T_b and S of 7.6 °C and 268 °C days respectively and accounted for 95 % of the variation. Boag (1985) similarly determined the duration of embryogenesis of another dorylaim nematode, *Longidorus elongatus* and his data is relatively linear (Fig. 2). The value of T_b was estimated as 8.5 °C, slightly higher than that for *X. diversicaudatum* even though *L. elongatus* has a more northerly distribution (Brown & Taylor, 1987). However, the estimated S requirement of *c.* 154 °C days was considerably less.

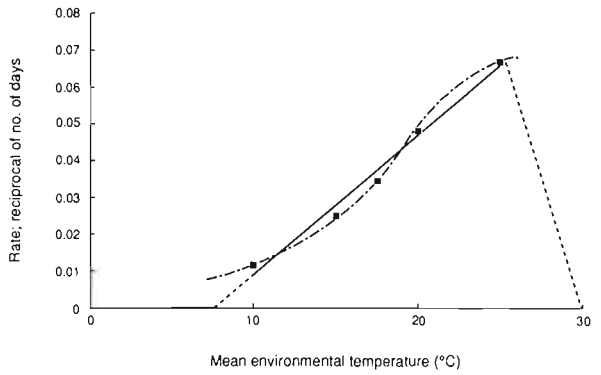

Fig. 1. *Relation between temperature and maximum rate of embryogenesis of* Xiphinema diversicaudatum. *(Data from Fig. 1 of Flegg, 1969).*

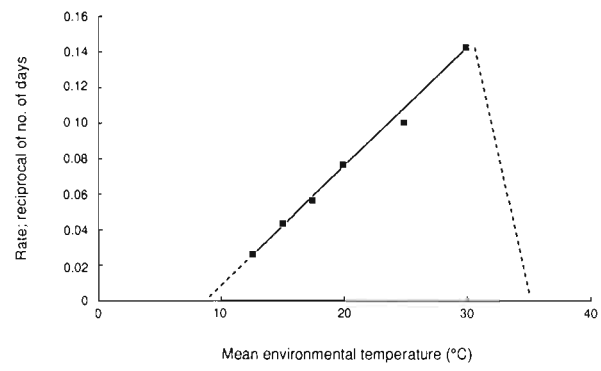

Fig. 2. *Relation between temperature and maximum rate of embryogenesis of* Longidorus elongatus. *(Data from Boag, 1985).*

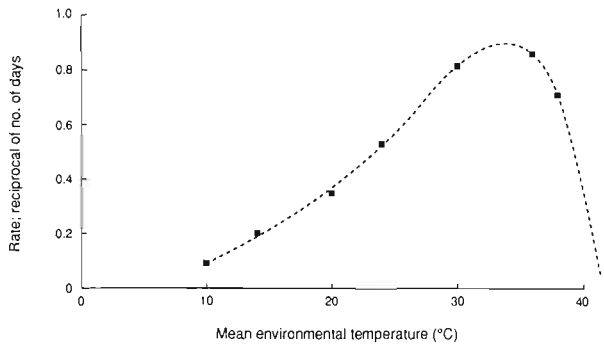

Fig. 3. *Relation between temperature and maximum rate of embryogenesis of* Aphelenchus avenae. *(Data from Table 1 of Taylor, 1962).*

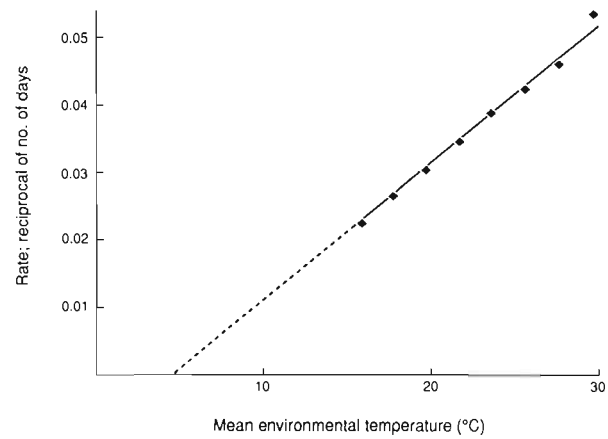

Fig. 4. *Relation between temperature and maximum rate of development from J2 to J2 of* Heterodera schachtii. *(The data is the mean of two populations and is from Fig. 2 and the text of Griffin, 1988).*

The thermal optima (T_o) were not accurately estimated by either Flegg or Boag but were around 25 °C and 30 °C respectively for *X. diversicaudatum* and *L. elongatus*. The thermal maxima (T_m) were < 30 °C for *X. diversicaudatum* and < 35 °C for *L. elongatus* as no development occurred at these temperatures.

Taylor (1962) assessed the duration of embryogenesis of *Aphelenchus avenae* at a range of temperatures. His data is also slightly more sigmoidal (Fig. 3). Fitting a straight line gave T_b as *c.* 8.2 °C and S as 31 °C days. The value of T_m is between 38 and 42 °C and of T_o between 30 and 36 °C, suggesting that *A. avenae* has a relatively wide temperature range.

Griffin (1988) determined the duration of development of *Heterodera schachtii* from invasive juvenile (J2) to first new J2 of the next generation at 2 °C intervals between 16 °C and 30 °C. His data (from his Fig. 2), when converted to rates of development (Fig. 4 here), gives a near perfect straight line. Back extrapolation to the temperature at which development duration is infinite gives a T_b of *c.* 4.6 °C and S of *c.* 502 °C days. This estimate of T_b is slightly less than his estimate (6.3 ± 0.48 °C), possibly partly because the data I used was derived from a histogram.

A detailed analysis in two experiments of development and egg production at four temperatures by *H. schachtii* was done by Caswell and Thomason (1991). Their data is quite variable but, using the most rapid development values gives approximate T_b values of 5 °C for development to egg laying and 8 °C for egg laying, an S value of 270 °C days up to egg laying and an additional requirement of 0.8 °C days for every egg produced.

Alston and Schmitt (1988) sought to determine the thermal requirements of *H. glycines* but their data is too variable to determine T_b and S. Pinkerton *et al.* (1991) used field observations to estimate for *Meloidogyne chitwoodi* values of T_b and of S of *c.* 5 °C and 950 °C days respectively for one generation, but only 1500 °C days were needed for development to the first hatched J2 from the second generation.

Embryogenesis in animal parasitic nematodes also appears to be governed by thermal time. Crofton and Whitlock (1964) assessed the duration of embryogenesis of two populations of the sheep parasite *Ostertagia circumcincta*. The results were rather variable but the fitted linear regression for the population from Bristol (UK) suggested a value of T_b of *c.* 4.1 °C and of S of *c.* 16.5 °C days (Fig. 5). For the population from Cornell (USA) the fitted values of T_b were 7.9 °C and of S were *c.* 14.6 °C days. The slope of the line for the Cornell population is especially uncertain but, with the lines fitted values of T_o were *c.* 24 °C and 28 °C for the Bristol and Cornell populations and of T_m were *c.* 35 °C and 40 °C respectively. However, there was a considerable temperature range between T_o and T_m where the rate of development was relatively constant. Overall, the results give the impression of a similar relationship between temperature and rates of development, but with the T_b, T_o and T_m values for the Cornell population being slightly increased compared with those of the Bristol population.

Data from similar studies with eggs of *Haemonchus contortus* from Cornell (USA) and Bristol (UK) (Crofton *et al.*, 1965) and from Scotland (UK) (Silverman & Campbell, 1958), were used to calculate rates of development and gave a series of relatively linear regressions (Fig. 6). The estimated values of T_b were *c.* 13.0, 9.1 and 6.6 °C for the Cornell, Bristol and Scottish populations and of S were 11.8, 13.4 and 14.9 °C days respectively (Table 1). The T_b and S values of the Cornell and Scottish populations were significantly different ($P < 0.001$). As T_b increased, presumably in response to selection by higher pasture temperatures, so the value of S appeared to decrease. Interestingly, Silverman and Campbell (1958) estimated T_o for the Scottish population as at least 37 °C, whereas T_m was estimated as 36 °C for the Bristol population and 40 °C for that from Cornell (Crofton *et al.*, 1965).

In one of the few studies on generation time Grewel (1991) determined the mean requirements (juvenile to egg hatch) of *Caenorhabditis elegans* over a range of temperatures. Re-plotting his data for the best food source *(Acinetobacter calcoaceticus)* shows (Fig. 7) a fitted value of T_b of *c.* 5.3 °C and an S of *c.* 43.1 °C days. The value of T_o was > 25 °C and of T_m < 28 °C.

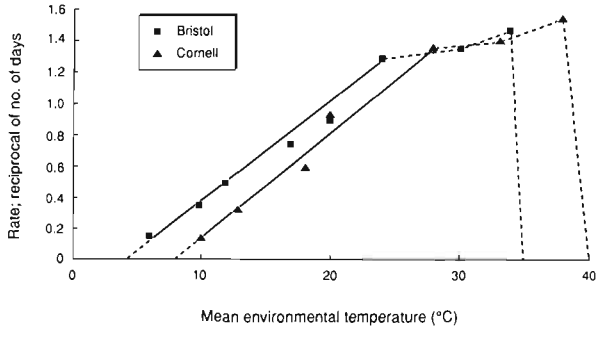

Fig. 5. *Relation between temperature and maximum rate of embryogenesis of* Ostertagia circumcincta. *(Data from Fig. 1 of Crofton and Whitlock, 1964).*

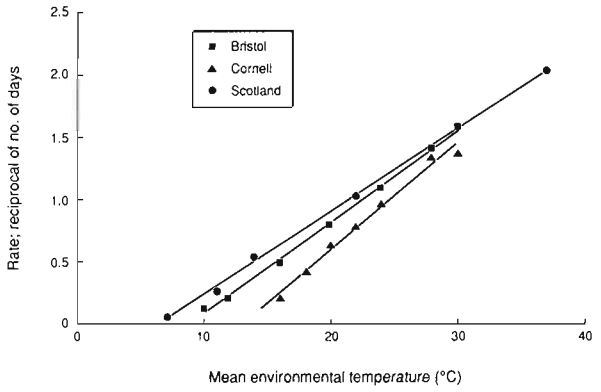

Fig. 6. *Relation between temperature and maximum rate of embryogenesis of three populations of* Haemonchus contortus. *(Data is from Fig. 1 of Crofton* et al., *1964 and from Silverman and Campbell, 1958).*

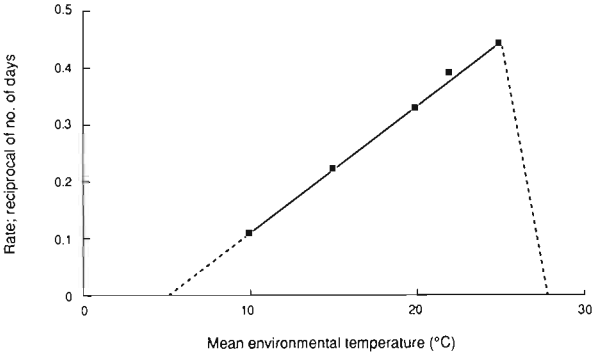

Fig. 7. *Relation between temperature and mean generation time of* Caenorhabditis elegans *feeding on* Acinetobacter calcoaceticus *var.* anitratus. *(Data from Table II of Grewel, 1991).*

Minimum thermal time requirements for embryogenesis and for one whole generation of *M. javanica*

Determining the value of T_b for a whole life cycle is relatively difficult and time consuming. It was therefore relevant to determine whether the values for embryogenesis and for the whole life cycle might be similar. A study was conducted with *M. javanica* and the results are reported here.

Materials and methods

Embryogenesis

The newly laid eggs needed to determine the thermal time requirements for embryogenesis were obtained by

allowing groups of three egg-laying females of *M. javanica* to deposit eggs in small Petri dishes (5 cm) containing a thin layer of 0.5 % water agar. The heads of the females were still buried within a small piece of root and, prior to transfer of the females to the agar, all eggs already laid were removed under a stereo binocular microscope. The duration of egg laying was varied from 2-17 h so that similar numbers of eggs (up to 40 per female) were laid at the different temperatures. The Petri dishes were partially sealed and maintained at a range of constant temperatures in incubators. Mean temperatures were measured with thermocouples and logged on a Grant " squirrel " data recorder. An accurate mercury thermometer (± 0.1 °C) was used to check and, where necessary, correct data from the thermocouples. The agar plates were inspected once (lower temperatures) or twice daily to detect the first juveniles to hatch. The temperatures used range from 17 to 31 °C and were covered in two separate studies.

Life cycle

The requirement for the minimum generation time was determined as described by Lahtinen *et al.* (1988) and Madulu and Trudgill (1994). Briefly, tomato plants cv. Moneymaker were each infested with *c.* 1000 juveniles of the population of *M. javanica* (from Tanzania) used in the embryogenesis studies. Groups of four plants were maintained in pots without drainage holes in water baths at a range of constant temperatures. Thermocouples buried in the pots measured the pot temperatures which were recorded and stored as for the embryogenesis studies. A few days before the first new juveniles were likely to hatch the soil in the pot was replaced by fine gravel and the plants, now in pots with drainage holes, returned to the water baths inside a second, close fitting pot without drainage holes. Each day the four pots at each temperature were irrigated with *c.* 400 ml of water, which was collected and any juveniles which had hatched extracted on a Baermann funnel. Collection of hatched juveniles continued for at least 3 days to confirm that hatch had started and numbers were progressively increasing. The data were from two experiments, one already reported by Madulu and Trudgill (1994).

Results

There were reasonable linear relationships over a 10 °C range between mean environment temperatures and maximum rates of embryogenesis and of development during a complete single generation (Fig. 8). The fitted values of T_b and S were 13.0 and 138 °C days for embryogenesis and 13.1 and 343 °C days for the whole life cycle. The S values were significantly different ($P < 0.05$) but the T_b values were not. The value of T_o was *c.* 27-28.5 °C. Between 27 and 31 °C rates of development were almost constant. The life cycle was not completed at a constant 34.7 °C.

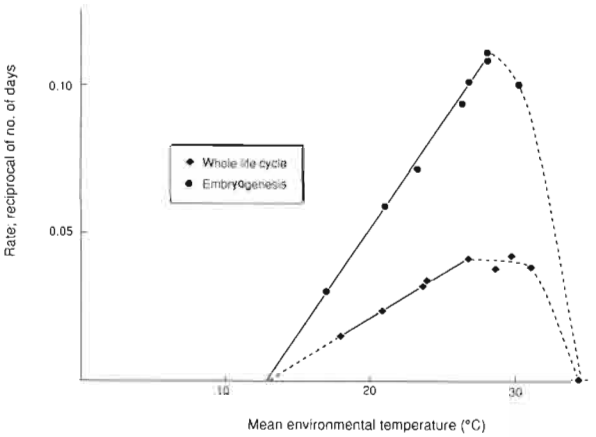

Fig. 8. *Relation between temperature and maximum rates of embryogenesis (o) and development from J2 to J2 of* Meloidogyne javanica.

Discussion

Do different process have the same value of T_b*?*

Mohamed *et al.* (1988 *b*) concluded that " the little evidence available (for plants) is consistent with a common value for T_b for different processes, so that values determined for seed germination can be used for other processes ". For nematodes, the limited evidence available is slightly more equivocal. Mugniéry (1977) estimated slightly different values of T_b for the maximum development rates of the different juvenile stages of *G. pallida* but similar values for juveniles of *G. rostochiensis*. The estimated values of T_b for embryogenesis of both species (Langeslag *et al.*, 1982) were, in spite of using a 50 % end-point, close to those estimated for development from J2 to first male (Mugniéry, 1977). Caswell and Thomason (1991) used the same value of T_b (8 °C) for both development of females and for egg production of *H. schachtii,* but my analysis suggests a value of < 5 °C for development to egg-laying females. Koshy and Evans (1986) observed at weekly intervals development durations for various stages of *H. cruciferae* and their data suggests a T_b of around 5.5 °C for production of adults and for completion of one generation.

The data presented here for *M. javanica* suggests a similar value of T_b of *c.* 13.0 to 13.0 °C for embryogenesis and for the whole life cycle (Fig. 8). On this basis, the S requirement for embryogenesis is 39 % of the total requirement, emphasising the large amount of development (or the slow rate) undertaken in tylenchid eggs. Overall, on the very limited evidence available, it seems possible that T_b values determined for embryogenesis are similar to those for whole life cycles.

Straight line or sigmoidal relationship

The practical and ecological importance of the cardinal values that can be derived from linear relationships has already been indicated. The already published data,

and that presented here suggests that for many nematode species maximum rates of embryogenesis and of development during a complete life cycle are linearly related to temperature over a considerable range between T_b and T_o. Above T_o, rates of development may change little over several °C, before decreasing rapidly to T_m (e.g. rate of embryogenesis of *Ostertagia circumcincta* (Fig. 5) and of development from inoculation of juveniles of *M. javanica* to hatch of the first juvenile of the next generation (Fig. 8)).

Entomologists generally apply a shallow sigmoidal curve to thermal time data, fitting it by eye (Guppy, 1969) or using a logistic equation (Andrewartha & Birch, 1954). Except at temperatures close to T_o and T_b deviations from a linear relation are often negligible and some authors (e.g. Kehat & Wyndham, 1972) have fitted straight lines. Conversely, other entomologists with apparently linear data fitted sigmoidal curves (e.g. Dean, 1974). Others (e.g. Larsen *et al.*, 1990) fitted both straight lines and curves. Baker (1980) considered some of the problems of using thermal time information to predict the timing of insect life cycles and concluded that there are two main sources of error; one in the calculations, the other in the observations. Proper estimation of the effective T_b (i.e. not influenced by the " tails " of the sigmoidal curve) is essential, although a small error does not have too serious effect as the estimates of T_b and of S are strongly negatively correlated. Other errors arise from using inappropriate temperature measurements (e.g. daily means from adjacent meteorological sites) and from a failure to recognise that, as units of effective temperature, day-degrees are physiological units of growth, not physical units of heat input.

Whether for nematodes the relationship is linear close to the value of T_b estimated by back-projection of a linear relationship is difficult to determine. Some of the available evidence suggests that rather than development continuing below T_b it is often arrested at temperatures slightly above T_b. Griffin (1988) determined a T_b for *H. schachtii* of *c.* 6.4 °C and my estimate, based on his data, was even lower (*c.* 4.6 °C). However, in his subsequent calculations he used a T_b of 8.0 °C as he argued that experience indicates that this is closer to the minimum soil temperature for hatch and invasion. Similarly Alston and Schmitt (1988) proposed a T_b of 5.0 °C for *H. glycines* even though development was not completed at 10 °C. Silverman and Campbell (1958) observed the death of most of the eggs of the Scottish population of *H. contortus* held at 7.2 °C and little hatching below 9.0 °C, although their data suggested a T_b of *c.* 6.6 °C. Also, Crofton *et al.* (1965) observed that eggs of the Cornell population did not hatch below 16 °C although the T_b estimated here was 13.0 °C. Boag (1985) similarly observed no hatch of eggs of *L. elongatus* at 10 °C even though T_b was estimated as *c.* 8.5 °C. With embryogenesis in insects, egg weight loss was shown to be greater at temperature close to T_b than at T_o. This led to the hypothesis that T_b is determined by energy reserves (see Howe, 1967). In contrast to the foregoing, eggs of the Bristol population of *H. contortus* hatched at 9.0 °C although T_b was estimated here as 9.1 °C. Some, but not all of these differences may be accounted for by errors in the estimation of T_b (and hence of S as their values are inversely correlated) emphasising the need for accurate estimates of development rates over a considerable range of temperatures.

All thermal time experiments contain certain biases due to errors and sometimes to external influences. Where data is variable due to external influences, those values influenced by sub-optimal conditions will tend to bias the regression towards a higher estimate of S and possible of T_b. Where, in water-bath experiments, the temperatures measured tend to differ from those experienced by the test organism due to thermal gain (at pot temperatures below air temperature) or loss (above air temperature) the errors will tend to increase rates of development at temperatures below, and decrease rates at temperatures above the ambient, thereby tending to convert a linear relationship into a sigmoidal one.

Another consideration which will complicate thermal time relationships is the considerable literature which suggest that at the low end of the temperature range adult size increases in a wide range of organisms including plants, ectothermic animals and bacteria (Atkinson, 1994). Such an effect would increase the S value at low, and decrease it at higher temperatures (tending to convert a sigmoidal into a linear relationship at values of T_c close to T_b).

Population heterogeneity for thermal requirements is a potentially important source of variation and hence a sigmoidal relationship. If, as proposed by Trudgill and Perry (1994) as T_b increases, S decreases, and hence the slope of the regression increases, then in heterogeneous populations the differential response to temperature of genotypes with different values of T_b will tend to produce a sigmoidal response when the relationship is based on minimum development durations. The sigmoidal response of *A. avenae* (Fig. 3) and to a lesser extent of *X. diversicaudatum* (Fig. 1) is, perhaps, a reflection of such heterogeneity. Often, close to the T_b based on a linear relationship, there is a high percentage mortality, probably resulting in selection for those individuals in a heterogeneous population which have a lower than average value of T_b (e.g. 80-90 % mortality of eggs at 15 °C of the Hemipteran bug *Nysius vinitor* with an estimated T_b of 14.5 °C; Kehat & Wyndham, 1972). Consequently, a linear relation may indicate a high degree of homogeneity but this, and the role of heterogeneity in the sigmoidal relationship needs testing.

Within species variation in T_b

The results of Silverman and Campbell (1958), Crofton and Whitlock (1964) and Crofton *et al.* (1965) show that within species variation, and probably selection for

changes in T_b can and do occur. Presumably, with *H. contortus* and *O. circumcincta* the Cornell populations were introduced with sheep from Europe but, subsequently, higher pasture temperatures have selected for increased values of T_b. Langeslag *et al.* (1982) also observed differences in T_b of *c.* 2.0 °C between populations of *G. pallida,* and considerable differences have been reported within species of crop plants (Mohamed *et al.,* 1988 *a*). However, in increasingly hot environments selection for elevated values of T_o and T_m, as was observed for both *H. contortus* (Fig. 6) and *O. circumcincta* (Fig. 5), seem likely to confer greater survival value than increases in T_b.

Relationship between T_b, S *and duration of development*

Increasing T_b without reducing S will increase D at all values of T_e (equation 1). In *H. contortus* the increased T_b of the Cornell compared with the Scottish population was associated with a decreased S (Fig. 6, Table 1). The consequence of this interaction is that at T_e = 35 °C the duration of embryogenesis of the Cornell population is slightly less than that of the Scottish population whereas at T_e = 15 °C eggs of the Scottish population develop more than twice as rapidly as those from Cornell.

A comparison of the effect of T_e on D in relation to embryogenesis of *L. elongatus* and *X. diversicaudatum* is instructive. *X. diversicaudatum* has a lower T_b than *L. elongatus* (7.0 compared with 8.5 °C) but a larger S (270 compared with 154 °C days; Table 1, Figs 1, 2). Consequently at T_e = 9.0 °C, D will be 135 days for *X. diversicaudatum* but 308 days for *L. elongatus*. In contrast at T_e = 18 °C, D will be 24.5 days for *X. diversicaudatum* but only 20.5 days for *L. elongatus*. Indeed, because of the interaction between T_b, S and T_e, the development rate of eggs of *L. elongatus* will be greater than that of *X. diversicaudatum* at all values of T_e between 10.5 °C and T_o.

The same interaction applies to seed germination. The grain crop sesame was shown to have a T_b of *c.* 16 °C and an S of *c.* 20 °C days compared with equivalent values of *c.* 2.6 °C and *c.* 80 °C days for barley (Angus *et al.,* 1981; Trudgill & Perry, 1994). Hence, at T_e = 18 °C sesame will take 10.0 days to germinate and barley 5.2 days whereas at 25 °C the relative D values are reversed with sesame calculated to take only 2.2 days to germinate and barley 3.6 days.

A similar analysis can be done for *M. hapla* and *M. javanica* (T_b *c.* 8.25 and 13.1 °C and S *c.* 554 and 343 °C days, respectively; Table 1, Fig. 9). At T_e = 21 °C their durations of development are similar (43-44 days) but *M. hapla* has the shorter life cycle at all temperatures below 21 °C and *M. javanica* has the shorter life cycle at all temperatures above 21 °C (Trudgill & Perry, 1994). Using a T_b of 5 °C Pinkerton *et al.* (1991) estimated S for the most rapid development of one generation of *M. chitwoodi* as 750-950 °C days, indicating that it is adapted to even cooler conditions than *M. hapla*.

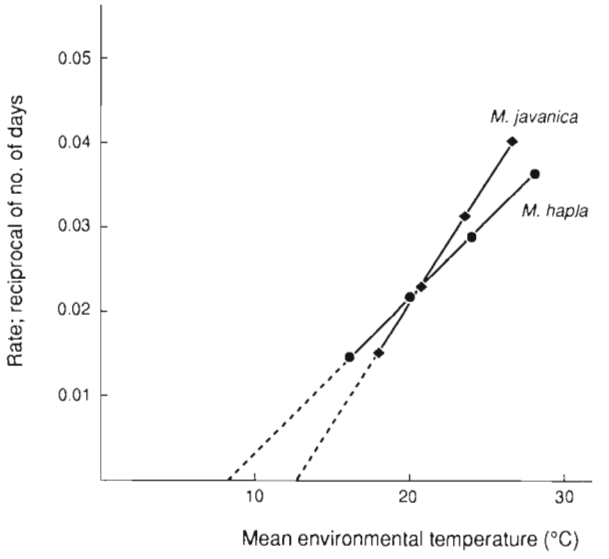

Fig. 9. *Relation between temperature and maximum rate of development from J2 to J2 of* Meloidogyne javanica *and* M. hapla. *Data from Lahtinen* et al. *(1988) and Madulu and Trudgill (1994).*

Ecological significance and use of T_b *and* S *values*

The nematode fauna of temperate and tropical regions differ (Das, 1970), with species adapted to their specific environments. There is evidence for both nematodes and plants that temperate species mainly have lower T_b values than comparable tropical species. Equally, where direct comparisons are possible (as with *Meloidogyne* spp.), lower T_b values are often associated with higher S values and vice-versa. The effect of decreasing S as T_b increases is to increase relative rates of development at all values of T_e between T_b and T_o. This interaction may be of fundamental ecological significance as it gives both the temperate and tropical species a selective advantage in the environments to which they are adapted and makes "good" ecological sense (Fig. 9).

A difficulty associated with the above analysis of the interaction between, T_b and S is the limited number of situations where direct comparisons between species appear to be valid. It appears (Angus *et al.,* 1981) that such comparisons are possible for the germination of seeds of crop plants. Embryogenesis of nematode eggs may appear, superficially, to be another process where direct comparisons across a wide range of species should be possible. However, this is not always so; tylenchid nematodes can be expected to have a higher S value than other nematodes because they undergo the first moult before hatching. Even so, the observation that the estimated S values of the animal parasitic species *H. contortus* and *O. circumcincta* (Table 1) were an order of magnitude less than those for tylenchid species with comparable values of T_b cannot be explained by this

difference. As S is the outcome of the amount of development divided by the rate of development then any differences in S are due either to differences in amounts of development or in rates of development, or to both.

The comparison between *M. hapla* and *M. javanica* (Fig. 9) of their T_b and S values is probably meaningful as both species undergo similar amounts of growth and development. However, on poorer hosts development rates are reduced (Anwar *et al.,* 1994), thereby increasing S. An alternative explanation, therefore, for the larger S value of *M. hapla* is that the tomato cv. Moneymaker, used in these experiments, is a poorer host for *M. hapla* than for *M. javanica.* However, a difference in host status should not influence the estimated value of T_b (unless it is relative differences between the T_b of the host and of the nematodes that is important). The corollary to the foregoing is that, for the same nematode species, host status differences can be described, and hosts compared in terms of the S values they confer on the nematode feeding upon them.

Equally, S values can be used to compare nematode species, those with small S values are likely to be " r " strategists and have relatively short life cycles and those with relatively large S values, and hence relatively large D requirements, will be " K " strategists (Southwood, 1981). If the amounts of growth can be determined, then differences in S values, given the same values of T_b, can be used to compare rates of growth and efficiencies of resource utilisation.

As " r" strategists are likely to have relatively small S values, then D will also be small. There are only a limited number of ways in which D can be decreased, and *M. javanica* and *M. hapla* show several such adaptations. They have reduced the S requirement associated with three of the juvenile stages by undergoing the first moult in the egg, and having two further non-functional juvenile stages. They are parthenogenetic, thereby eliminating the S component of the life cycle associated with mating. And they have optimised their relationship with their hosts to maximise food availability and growth rates.

Thermal time information also provides useful practical information. Ferris *et al.* (1978) used it as a basis of a population dynamics and yield loss model. Tiilikkala *et al.* (1988) used it to assess whether *M. hapla* could become established in Finland, and Langeslag *et al.* (1982) sought to use it as a basis for the cultural control of potato cyst nematodes. Also, there have been many field-based studies where T_b has been roughly estimated (e.g. Griffin, 1985).

Currently, there is interest in developing cold adapted strains of entomopathogenic nematodes which function well at lower temperatures (< 15 °C). Ignoring the complication of the bacterial component, it can be predicted that, provided sufficient heterogeneity is present, selection for such strains should be possible. However, they will probably not perform as well in warm soils as unadapted strains. Equally, they will be less effective at low temperatures than are unadapted strains at higher temperatures and, to prevent genetic drift, they will have to be cultured at relatively low temperatures. If an inappropriate screen is used based on generation time rather than infectivity at low temperature, then the effect may be to select smaller nematodes (smaller S) rather than ones with a lower T_b.

There is therefore, good reason to establish the relevance of the thermal time relationship to nematodes of agricultural importance and to understand the requirements of the more important species. Much remains to be done, including a study of the mechanisms involved and their genetic basis. Phase transition temperatures of lipids in phospho-lipid membranes (Lyons *et al.,* 1974) may be involved in determining T_b and the value of S if membrane efficiency is inversely correlated with lipid melting temperatures. More is needed to determine the thermal time investment in each egg, as this is also likely to vary greatly between r and K strategists and the effects of environment on adult size need further study. Overall, thermal time information could help refine broader ecological approache such as that suggested by Bongers (1990) in his maturity index. If rates of development and of T_b are similar, then differences in adult size reflect differences in S, and hence whether species within families are more r or more K (coloniser or persister) strategists. Lastly, all the work considered here is based on one generation under constant temperatures, and thus may be appropriate because soil temperatures are relatively stable, but with other organisms there have been many studies under natural, fluctuating temperatures (e.g. Pierre, 1991), with modelling extended to cover several, overlapping generations.

Acknowledgements

This work was supported by the Scottish Office Agriculture and Fisheries Department. Drs G. Squire and D. Mugniéry are thanked for critical comments.

References

ALSTON, D. G. & SCHMITT, D. P. (1988). Development of *Heterodera glycines* life stages as influenced by temperature. *J. Nematol.,* 20 : 366-372.

ANDREWARTHA, H. G. & BIRCH, L. C. (1954). *The distribution and abundance of animals.* Chicago, USA, The University of Chicago Press, 782 p.

ANGUS, J. F., CUNNINGHAM, R. B., MONCUR, M. W. & MACKENZIE, D. H. (1981). Phasic development in field crops. I. Thermal response in the seedling phase. *Field Crops Res.,* 3 : 365-378.

ANWAR, S. A., TRUDGILL, D. L. & PHILLIPS, M. S. (1994). The contribution of variation in invasion and development rates of *Meloidogyne incognita* to host status differences. *Nematologica* (in press).

ATKINSON, D. (1994). Temperature and organism size – a biological law for ectotherms. *Adv. ecol. Res.,* 25 : 1-58.

BAKER, K. (1980). Some problems in using meteorological data to forecast the timing of insect life cycles. *EPPO Bull.,* 10 : 83-91.

BOAG, B. (1985). Effect of temperature on the times of hatching of eggs of the plant parasitic nematode *Longidorus elongatus*. *Nematol. medit.,* 13 : 61-66.

BONGERS, T. (1990). The maturity index : an ecological measure of environmental disturbance based on nematode species composition. *Oecologia,* 83 : 14-19.

BROWN, D. J. F. & TAYLOR, C. E. (1987). Comments on the occurrence and geographical distribution of longidorid nematodes in Europe and the Mediterranean region. *Nematol. medit.,* 15 : 333-373.

CASWELL, E. P. & THOMASON, I. J. (1991). A model of egg production by *Heterodera schachtii* (Nematoda : Heteroderidae). *Can. J. Zool.,* 69 : 2085-2088.

CROFTON, H. D., WHITLOCK, J. H. & GLAZER, R. A. (1965). Ecology and biological plasticity of sheep nematodes. II. Genetic × environmental plasticity in *Haemonchus contortus* (Rud, 1803). *Cornell Vet.,* 55 : 251-257.

DAO, D. F. (1970). Climatic influences on the distribution pattern of plant parasitic and soil inhabiting nematodes. *Meded. LandbHogesch. Wageningen,* 70 : 1-181.

DEAN, G. J. (1974). Effect of temperature on the cereal aphids *Metopolophium dirhodum* (Wlk.), *Rhopalosiphum padi* (L.) and *Macrosiphum avenae* (F.) (Hem., Aphididae. *Bull. ent. Res.,* 63 : 401-409.

FERRIS, H., DU VERNAY, H. S. & SMALL, R. H. (1978). Development of a soil temperature data base on *Meloidogyne arenaria* for a simulation model. *J. Nematol.,* 10 : 39-42.

FLEGG, J. M. (1969). The effects of temperature on the embryogeny of *Xiphinema diversicaudatum*. *Nematologica,* 15 : 285-296.

GARCIA-HUIDOBRO, J., MONTEITH, J. L. & SQUIRE, G. R. (1982). Time, temperature and germination of pearl millet. *J. exp. Botany,* 33 : 288-296.

GREET, D. N. (1978). The effect of temperature on the life cycle of *Panagrolaimus rigidus* (Schneider). *Nematologica,* 24 : 239-242.

GREWEL, P. S. (1991). Influence of bacteria and temperature on the reproduction of *Caenorhabditis elegans* (Nematoda : Rhabditidae) infesting mushrooms *(Agaricus bisporus). Nematologica,* 37 : 72-72.

GRIFFIN, G. D. (1988). Factors affecting the biology and pathogenicity of *Heterodera schachtii* on sugar beet. *J. Nematol.* 20 : 396-404.

GUPPY, J. C. (1969). Some effects of temperature on the immature stages of the armyworm, *Pseudetatia unipuncta* (Lepidoptera : Noctuidae), under controlled conditions. *Canad. Entomologist,* 101 : 1320-1327.

HOWE, R. W. (1967). Temperature effects on embryonic development. *A. Rev. Ent.,* 12 : 15-42.

JONES, F. G. W. (1977). Temperature and development on *Mononchus aquaticus*. *Nematologica,* 23 : 123-125.

KEHAT, M. & LYNDHAM, M. (1972). The influence of temperature on development, longevity and fecundity in the Rutherglen bug, *Nysius vinitor* (Hemiptera : Lygaeidae). *Austr. J. Zool.,* 20 : 67-78.

KOSHY, P. K. & EVANS, K. (1986). Hatching from cysts and egg sacs of *Heterodera cruciferae* and effects of temperature on hatching and development on oilseed rape. *Ann. appl. Biol.,* 109 : 163-171.

LAHTINEN, A. E., TRUDGILL, D. L. & TIILIKKALA, K. (1988). Threshold temperature and minimum thermal time requirements for the complete life cycle of *Meloidogyne hapla* from northern Europe. *Nematologica,* 34 : 443-451.

LANGESLAG, M., MUGNIÉRY, D. & FAYET, G. (1982). Développement embryonnaire de *Globodera rostochiensis* et *G. pallida* en fonction de la température en conditions contrôlées et naturelles. *Revue Nématol.,* 5 : 103-109.

LARSEN, K. J., MADDEN, L. V. & NAULT, L. R. (1990). Effect of temperature and host plant on the development of the blackface hopper. *Ent. exp. & appl.,* 55 : 285-294.

LEACH, L., TRUDGILL, D. L. & GAHAN, P. B. (1986). Influence of food and temperature on the development and moulting of *Goodeyus ulmi* (Nematode : Rhabditida). *Nematologica,* 32 : 216-221.

LYONS, J. M., KEITH, A. D. & THOMASON, I. J. (1974). Temperature-induced phase transitions in nematode lipids and their influence on respiration. *J. Nematol.,* 7 : 98-104.

MADULU, J. & TRUDGILL, D. L. (1994). Influence of temperature on *Meloidogyne javanica*. *Nematologica,* 40 : 230-243.

MOHAMED, H. A., CLARK, J. A. & ONG, C. K. (1988 *a*). Genotypic differences in the temperature responses of tropical crops. I. Germination characteristics of groundnut (*Arachis hypogaea* L.) and pearl millet (*Pennisetum typhoides* S. & H.). *J. exp. Botany,* 39 : 1121-1129.

MOHAMED, H. A., CLARK, J. A. & ONG, C. K. (1988 *b*). Genotypic differences in the temperature responses of tropical crops. II. Seedling emergence and leaf growth of groundnut (*Arachis hypogaea* L.) and pearl millet (*Pennisetum typhoides* S. & H.). *J. exp. Botany,* 39 : 1129-1135.

MUGNIÉRY, D. (1978). Vitesse de développement, en function de la température de *Globodera rostochiensis* et *G. pallida* (Nematoda : Heteroderidae). *Revue Nématol.,* 1 : 3-12.

PIERRE, J. S. (1991). An estimation of thermodependent development rates of the larval instars of the grain aphid *Sitobion avenae* F., under naturally fluctuating temperatures conditions. *VIth Symposium über Schadenerreger in der Getreideproduktion, Dec. 1990, Halle, Deutschland :* 2-7.

PINKERTON, J. N., SANTO, G. S. & MOJTAHEDI, H. (1991). Population dynamics of *Meloidogyne chitwoodi* on Russet Burbank potatoes in relation to degree-day accumulation. *J. Nematol.,* 23 : 285-290.

RAMIN, A. A. & ATHERTON, J. G. (1991). Manipulation of bolting and flowering in celery (*Apium graveolens* L. *verdulce*). II. Juvelinity. *J. hort. Sc.,* 66 : 709-717.

SILVERMAN, P. H. & CAMPBELL, J. A. (1958). Studies on parasitic worms of sheep in Scotland. I. Embryonic and

larval development of *Haemonchus contortus* at constant conditions. *Parasitology,* 49 ; 23-28.

SINGH, M. & SHARMA, S. B. (1994). Temperature effects on development and reproduction of *Heterodera cajani* on pigeon pea. *J. Nematol.,* 26 : 241-248.

SOUTHWOOD, T. R. E. (1981). Binomic strategies and populations parameters. *In :* May, R. M. (Ed.). *Theoretical ecology, principles and applications, 2nd Ed.* New York, Blackwell Scientific Publications : 30-52.

TAYLOR, D. P. (1962). Effect of temperature on hatching of *Aphelenchus avenae* eggs. *Proc. helminth. Soc. Wash.,* 29 : 52-54.

TRUDGILL, D. L. & PERRY, J. N. (1994). Thermal time and ecological strategies – A unifying hypothesis. *A. appl. Biol.* (in press).

TYLER, J. (1933 *a*). Development of root-knot nematodes as affected by temperature. *Hilgardia,* 7 : 391-414.

TYLER, J. (1933 *b*). Egg output of the root-knot nematode. *Proc. helminth. Soc. Wash.,* 5 : 49-54.

WIGGLESWORTH, V. B. (1972). *The principles of insect physiology. 7th Ed.,* London Chapman & Hall, 827 p.

WILLIAMS, C. T. & WRATTEN, S. D. (1987). The winter development, reproduction and lifespan of viviparae of *Sitobion avenae* (F.) (Hemiptera : Aphididae) on wheat in England. *Bull. ent. Res.,* 77 : 19-34.